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Gabriela Mataloni

To cite this article: Gabriela Mataloni (2016): Diversity patterns of plankton communities in Tierra del Fuego peat bog pools as sentinels of climate change, Biodiversity, DOI: 10.1080/14888386.2016.1180639

To link to this article: <http://dx.doi.org/10.1080/14888386.2016.1180639>



Published online: 04 May 2016.



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Diversity patterns of plankton communities in Tierra del Fuego peat bog pools as sentinels of climate change

Gabriela Mataloni^{a,b}

^aInstituto de Investigación e Ingeniería Ambiental (3iA), Universidad Nacional de San Martín, San Martín, Prov. de Buenos Aires, Argentina;

^bConsejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), Argentina

ABSTRACT

Although they contribute a significant proportion of peatlands diversity, peat bog pools are poorly surveyed and understood. In this review, the Rancho Hambre peat bog is taken as a study case to investigate the role of climate-related features in setting the environment of pools and in shaping the structure and dynamics of plankton communities. An interpretation model is proposed in which the interaction of pool morphometry and hydrological connectivity with temperature and precipitation lead to distinct pool types according to their size and trophic status. Molecular diversity spatial patterns for small-sized eukaryotes and prokaryotes coincide with those detected for larger planktonic communities studied by traditional morphology-based taxonomy, all of them supporting this environmental characterisation together with distinct trophic web compositions. Small, acidic ombrotrophic pools showed significantly poorer communities and bacterial phylogenetic clustering, suggesting a stronger environmental filtering that could be enhanced by a lowering water table depth driven by local climate change.

ARTICLE HISTORY

Received 27 January 2016

Accepted 17 April 2016

KEYWORDS

Plankton; community ecology; molecular diversity; peat bogs; climate change; Tierra del Fuego

Introduction

Peat bogs, ecosystem services and biodiversity

Peatlands are a wetland type characterised by the capacity of accumulating dead organic material (peat) under particular environmental conditions leading to permanent water logging, such as low temperatures and abundant, evenly distributed precipitations. Globally, they hold one third of the soil carbon and about 10% of the freshwater, involving an area of about 4 million km² (Joosten and Clarke 2002). The areas of the peatland wherein peat is actively produced, called mires, can be dominated by different plant species and are commonly classified into fens and peat bogs. The latter, frequently dominated by *Sphagnum* spp. mosses, typically evolve from concave minerotrophic fens partially fed by nutrient-richer water that has been in contact with mineral soil, to raised ombrotrophic bogs fed exclusively by nutrient-poor, acidic precipitation water (Roig and Roig 2004). Although the most conspicuous ecosystem services provided by peat bogs relate to their regulating functions, i.e. carbon and freshwater storage, these ecosystems are also much valued as biodiversity reservoirs (Iturraspe 2010; Rydin

and Jeglum 2006) on account of the highly specialised biota inhabiting them. Furthermore, from a microbiological viewpoint, ombrotrophic bogs are recognised as the most reliable natural records of past environmental and climatic changes, as their only inputs are atmospheric in origin (Puglisi et al. 2014). Despite this, their microbial diversity has only been partially surveyed, as most work has focussed on the 'terrestrial' matrix dominating the landscape in many peatlands, and dealt mostly with components of the microbial loop (Andersen, Chapman, and Artz 2013; Mieczan and Tarkowska-Kukuryk 2013 and references therein). Also, for many years now the phytoplankton diversity of bog pools in relation to abiotic features has been studied in peatlands around the Northern Hemisphere (Bórics et al. 2003; Coesel 1986; Cosandey 1964; Hosiaisuoma 1975; Kulikovskiy 2009 and references therein; Machová-Černá and Neustupa 2009; among many others). Only of late has the overall eukaryotic diversity been investigated with molecular methods (Lara et al. 2011) whilst the goal of integrating the qualitative and quantitative study of the different components of the trophic web, as proposed by Gilbert and Mitchell (2006), has not been achieved yet.

The peat bogs from Tierra del Fuego

Although the Northern Hemisphere hosts most peatlands around the world, Lindsay et al. (1988) defined the 'Magellanic tundra complex' as the southernmost area of extensive peat bog development, which encompasses mainly the island of Tierra del Fuego. In particular, the Argentinean section of the island (Tierra del Fuego province) engages an area of about 2700 km² of peatlands (Iturraspe 2010) storing a water volume which amounts to 20 times that of all glaciers in the province (Wetlands International 2015). Historically, Fuegian peat bogs have been studied from a mineralogical viewpoint (Auer 1965; Guiñazú 1934; Rabassa, Coronato, and Roig 1996). Only lately has attention been paid to the fact that their functioning as carbon sinks can be reversed by disturbance (Pena 2009) and that it largely depends on the water table depth, which in turn can be altered by draining or by changes in the regional hydrology as a consequence of climate change (Iturraspe 2010).

In 2005, the International Mire Conservation Group (IMCG) emphasised the need to study the biodiversity and functioning of these systems and to develop baseline data to enable the monitoring of future changes (IMCG 2005). As of 2011, the Government of the Tierra del Fuego Province established preservation criteria for the peatlands, including the concentration of extraction activities in already degraded peatlands, with an aim to preserve their pristine status in the rest of the province.

A case study: the pools of the Rancho Hambre peat bog

The Rancho Hambre peat bog belongs to the Tierra Mayor Valley Natural Reserve, which extends along 50 km amidst the *Nothofagus* wood-covered slopes of the southernmost Andean ranges. It has been classified as a typical dome-shaped ombrotrophic peat bog, fed by precipitation and snowmelt (Roig and Roig 2004). Its surface hosts a large number of shallow (depth < 2 m) water bodies, and Larsifashaj River meanders along the southern margin of the dome. Here, Mataloni and Tell (1996) studied the structure of the phytoplankton communities from five pools and the river in relation to their morphometric and abiotic features. Unexpectedly high α - and β -diversities (those of each water body and between them, respectively) were revealed along with the relation between floristic composition and water body morphometry, while dominance of certain taxonomic groups strongly correlated with pH (Mataloni and Tell 1996). These findings are comparable to previous ones from peat bog pools in the Northern Hemisphere (Coesel 1986; Pautou and Baier 1983). More recently, studies including whole microbial communities

demonstrated their usefulness in characterising the environmental conditions and assessing the effect of disturbances on the *Sphagnum*-dominated terrestrial matrix of peatlands (Gilbert and Mitchell 2006). Therefore, new questions regarding the ecology of Fuegian peat bog pools arose: (i) How do climate-related abiotic features modify the environmental conditions of the pools? (ii) How does this shape the structure and dynamics of plankton communities and their interactions? and (iii) What is the potential of these communities as indicators of climate-related environmental changes?

The environment

Between 2008 and 2010, a comprehensive research project in Rancho Hambre involved the sampling of five pools (RH1 to RH5) standing for distinct morphometrical features over two consecutive ice-free periods (Figure 1). One to four sampling stations were established in each pool according to size, in each of which a set of limnological features was measured: water level, temperature, conductivity, pH, dissolved O₂, total hardness, transparency, total N and P, NO₃-N, NH₄-N, PO₄-P and dissolved organic carbon (DOC). Planktonic heterotrophic bacteria (HB), phytoplankton size fractions, heterotrophic flagellates (HF), ciliates and five metazooplankton taxonomic and functional groups (micro-filtering nauplii, micro-filtering rotifers, omnivorous copepods, filtering cladocerans and predators) were quantified, and the diversity of nano- and microphytoplankton, ciliates and metazooplankton groups was studied in detail (Quiroga et al. 2013). Also, a set of meteorological features was continuously measured for the entire system: precipitation, wind direction and speed, temperature of the air, peat and water in the smallest and largest pools (RH3 and RH4, respectively).

Strong, constant winds coinciding with the pools fetch accounted for highly homogeneous abiotic features and plankton distribution even in the largest pool (González Garraza et al. 2012; Quiroga et al. 2013). Pool morphometry strongly influenced patterns of water temperature variation, as small RH3 showed higher maximum temperatures and a wider diurnal range than large RH4. Also, hydrological connectivity played a key structuring role: large, deeper RH1 and RH4 had superficial inflows and outflows and showed a steadier water level and minerotrophic features (mildly acidic, slightly harder, DOC-poorer waters), whilst shallow pools were clearly ombrotrophic (acidic, softer, DOC-richer waters) and large, isolated RH2 showed an intermediate trophic status and the most variable water level. These conditions set an environmental diversity pattern characterised by two variation sources: on one hand, pH and trophic status imposed a spatial variation source, while interactions

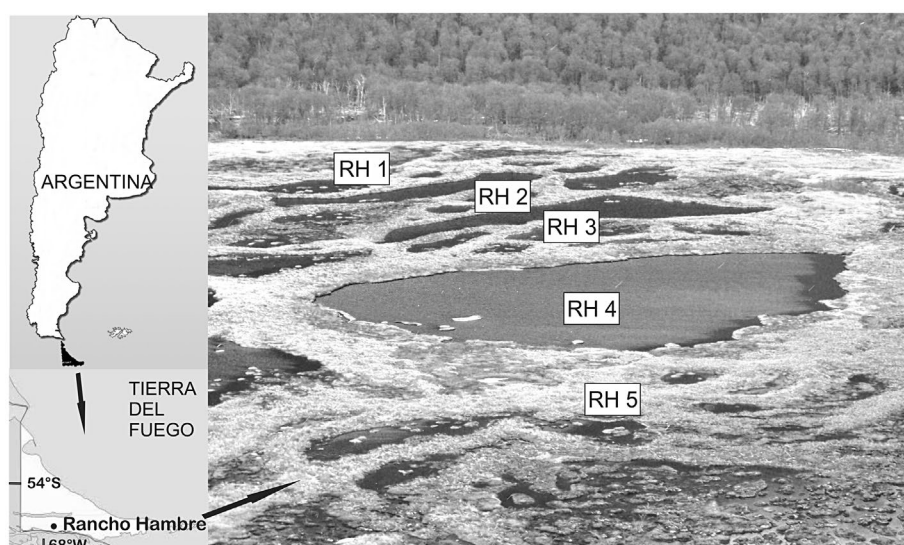


Figure 1. Location map of the Rancho Hambre peat bog and view of the studied water bodies (RH1–RH5).

among temperature and water level, reflected by conductivity and nutrient concentrations, set a seasonally driven source for environmental variation.

Environmental drivers of community structure

The detailed analysis of the structure and dynamics of the phytoplankton and their relation to environmental features allowed testing of the hypothesis that taxonomic composition would show a spatial pattern driven by landscape-controlled features such as pH and trophic status, while temperature and weather-dependent features would account for seasonal changes in abundance and structure. Results showed that a high number of green algae and diatoms strongly preferred minerotrophic pools (see Mataloni, González Garraza, and Vinocur 2015 for complete taxonomic list) and largely made up for their high species richness (Figure 2). Nonetheless, low Jaccard similarity indices (0.31–0.54) revealed striking differences in the species composition of the nano- and microphytoplankton among pools, albeit reaching maximum values among pools with the same size and trophic status and a minimum among the two closest yet hydrologically isolated and environmentally disparate pools. Whilst overall community resemblance among pools of a same trophic status suggests deterministic processes driving the high-level taxonomic composition of pools, the low similarity at species level reveals a severe constraint on propagule dispersion among pools of similar features, as demonstrated by Černá (2010) for a Czechian peat bog, and allows for stochastic forces to play a key role in driving the species composition of a given pool. In turn, interplay amongst deterministic and stochastic processes resulted in the high beta-diversity characteristic of these systems (Beadle,

Brown, and Holden 2015). These findings are consistent with those of Soininen et al. (2007), who found that plankton communities of boreal wetland ponds were strongly spatially structured even across small spatial scales.

According to Mataloni, González Garraza, and Vinocur (2015) canonical correspondence analysis (CCA) ordinated abundances and species richness of taxonomic groups in relation to abiotic features with first two axes explaining 84.7% of species-environment relation ($p < 0.002$). Abundances of various taxonomic groups were ordinated along Axis 1, which represented seasonal environmental variation through the high influence of temperature and conductivity, while Axis 2 discriminated species richness and represented spatial variation through pH, in accordance with the results discussed above. These results as a whole allowed the proposal of an interpretative model to hypothesise the ways in which this landscape-driven environmental variability shapes plankton communities in peat bog pools (Figure 3). According to this model,

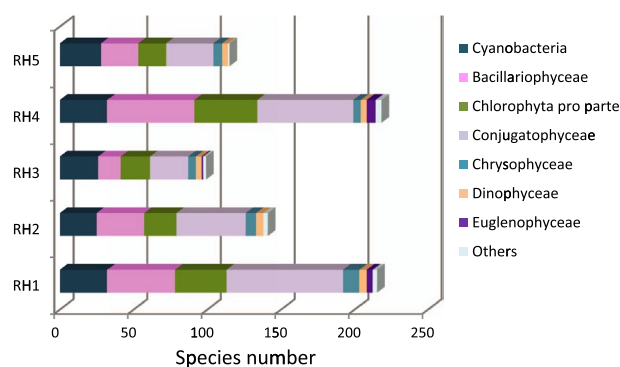


Figure 2. Partitioning into the major taxonomic groups of the total phytoplankton species richness recorded over two years in each pool.

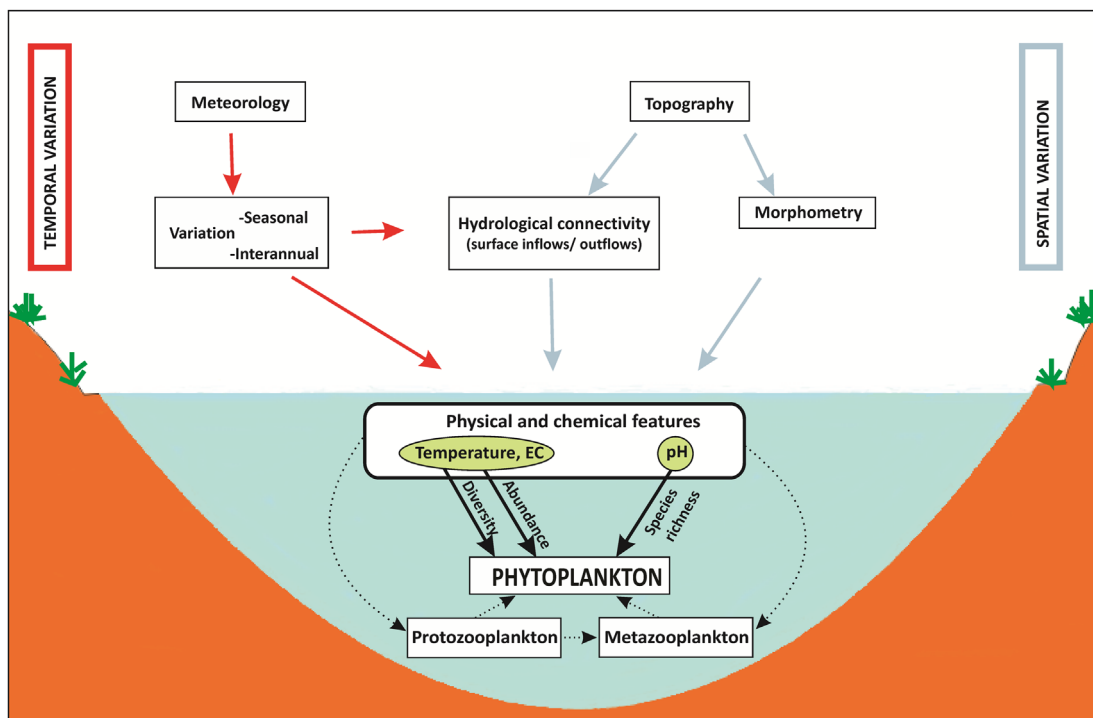


Figure 3. Proposed interpretative model of the pathways through which landscape-driven and temporal sources of environmental variability shape plankton communities in peat bog pools. EC: electric conductivity. Red (dark grey) arrows stand for temporal variability. Light blue (light grey) arrows stand for spatial variability. Dotted arrows stand for putative trophic interactions as discussed in Quiroga et al. (2013). After Mataloni, González Garraza, and Vinocur (2015). © Springer. (Published with permission from Springer.)

topography is the main source of spatial environmental variability through pool morphometry and hydrological connectivity, which largely account for trophic status of the pools. Connectivity, in turn, is subjected to meteorological variability, as it depends on water table depth and ultimately on hydric balance (Iturraspe 2010), and interplay of these features is the main driver of the abiotic environment of pools, which in turn largely shapes phytoplankton features such as species richness and composition (Bórics et al. 2003) and even cell size structure of given taxonomic groups (Neustupa, Veselá, and Štátný 2013).

Trophic web structure

Whilst studies on the trophic web structure in peatlands have been conducted mostly in the water environment among *Sphagnum* mosses (Mieczan 2007; Mitchell et al. 2003), microalgal community composition can change dramatically over a short (3.2 m) gradient extending from open water to the surrounding mosses (Mataloni 1999); therefore some aspects of plankton communities from Tierra del Fuego bog pools compare best to that of plankton from humic bogs and lakes (Graham et al. 2004; Tadonlécé, Planas, and Lucotte 2005). Abundances of most plankton trophic compartments were comparable or slightly higher than those observed in the aforementioned

environments, and strongly correlated with temperature. A principal component analysis (PCA) based on abundances of plankton communities in every pool and date revealed seasonality as the main source of variance, with all early spring samples clearly separated from the rest and characterised by low abundances of virtually all trophic compartments excepting nauplii (Quiroga et al. 2013). In turn, summer and autumn samples differed according to pool size, with smaller water bodies characterised by high abundances of mixotrophic flagellates and rotifers, and larger ones with high abundances of autotrophic phytoplankton and crustaceans. Such differences became even more significant as regards to plankton biomass. Figure 4 shows how average biomass values for all pools in October evolved into different community structures in small and large pools by mid-summer (February samples), strongly suggesting different C pathways through the trophic web in these two types of environments. Such differences seem to be dictated by distinct pool size-driven patterns of water temperature variation, as temperature is known to influence growth and development of metazooplankton (Cook et al. 2007), a particularly rich community in these fishless systems (Beadle, Brown, and Holden 2015) acting as top predators and therefore able to exert a cascading effect on community structure of lower levels. Indeed, the smaller metazooplankton biomass in small pools seems to interact with environmental features such as DOC and nutrient

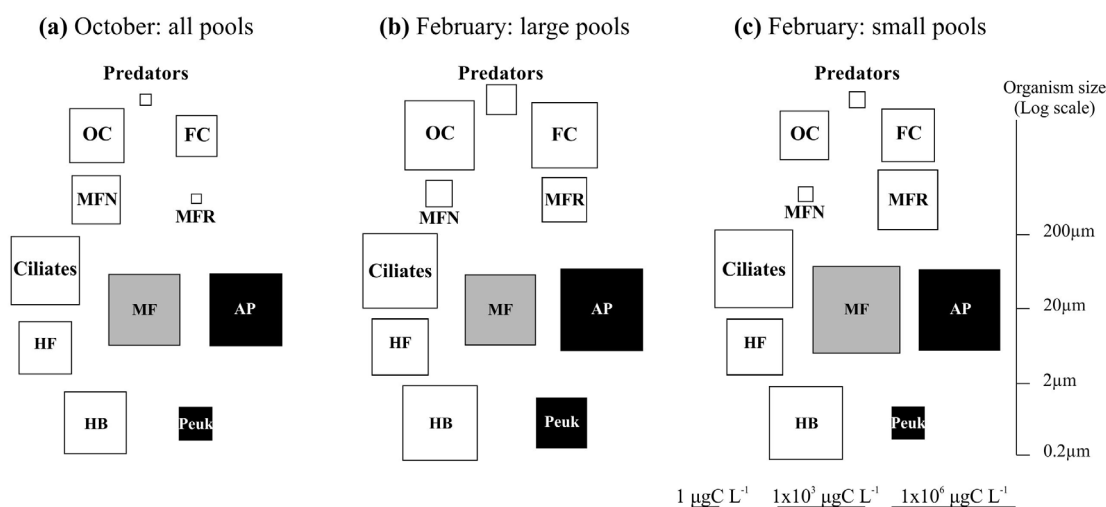


Figure 4. Averages of abundance-based biomass of plankton communities from Rancho Hambre pools in (a) early spring (October) samples from all pools, (b) late summer (February) samples from large pools (RH1, RH2, RH4) and (c) late summer (February) samples from small pools (RH3, RH5). Box areas are proportional to the biomass (\log_{10} -transformed) of the plankton trophic compartments. HB: heterotrophic bacteria; Peuk: picoeukaryotic algae; AP: autotrophic phytoplankton; HF: heterotrophic flagellates; MF: mixotrophic flagellates; MFR, micro-filtering rotifers; MFN: micro-filtering nauplii; OC: omnivorous copepods; FC: filtering cladocerans. Nutrition mode: white, heterotrophic; grey, mixotrophic; black, autotrophic. After Quiroga et al. (2013). © Oxford University Press. (Published with permission from Oxford University Press.)

concentrations to favour phytoplankton dominance by mixotrophic flagellates, as observed by Saad et al. (2013) for other Fuegian and Patagonian environments, which in turn can exert a significant grazing pressure on pico-sized algae (Quiroga et al. 2013; Raven, Finkel, and Irwin 2005).

Molecular diversity patterns

Prokaryotes

Throughout the 2008–2010 research project, the traditional morphology-based taxonomical approach was used in order to analyse the $>2 \mu\text{m}$ fraction on the phytoplankton, ciliates and metazooplankton. Nonetheless, the diversity and spatial distribution patterns of HB, as well as forces driving them, remained unknown. In November 2012, triplicate bacterioplankton samples were taken from each of the same five pools in Rancho Hambre along with the same set of abiotic variables formerly studied, and analysed using high-throughput barcode amplicon sequencing in order to test whether prokaryotes reflected environmental diversity in the same manner as large eukaryotic plankton. A total of 897 bacterial operational taxonomic units (OTUs, sequences binned at a 97% similarity cut-off) were identified in 30,225 sequences (Quiroga et al. 2015). Although most taxa among them were rare (72% of OTUs occurred in a single sample), 10 OTUs were present in more than 80% of samples and belonged to the *Proteobacteria* (38% of all sequences, mostly *Betaproteobacteria*) and *Actinobacteria* (12% of all sequences). Bacterial communities from the

same pool were both highly similar and significantly different from those of other pools. This was not surprising, as results of a permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarities showed that the variation in bacterial community structure was largely explained by pH and also by nutrient status, which were known to be highly homogeneous within each pool (González Garraza et al. 2012).

Minerotrophic pools (RH1, RH4) had higher bacterial diversity than ombrotrophic pools. This was in agreement with previous studies comparing ombrotrophic bogs vs. minerotrophic fen environments in the Northern Hemisphere (Lin et al. 2012; Opelt et al. 2007), which ascribed the low diversity found in the former to their more extreme acidic conditions. Moreover, among the bacterioplankton communities studied in Rancho Hambre, only those of ombrotrophic pools showed phylogenetic clustering. As this would indicate closely related species sharing special traits that allow them to persist in a given habitat (Horner-Devine and Bohannon 2006), it was concluded that environmental conditions in these pools would impose a stronger ecological filter in comparison with minerotrophic pools (Quiroga et al. 2015).

Small-sized eukaryotes

During the 2008–2010 study of Rancho Hambre peat bog pools, different epifluorescence microscopy techniques were used to enumerate pico-sized ($<2 \mu\text{m}$) organisms. HB and flagellates were counted in DAPI-stained samples (Quiroga et al. 2013), whilst autofluorescence of

photosynthetic pigments was used to analyse the picophytoplankton. Interestingly, this fraction was composed only of taxonomically unidentifiable eukaryotes, as confirmed by Quiroga et al. (2015), while the smallest individuals composing the nanophytoplankton (<3 µm) which lacked discriminating morphological traits could only be identified at a very coarse level, despite the fact that these organisms are known to exhibit a large diversity (Richards et al. 2005).

With an aim at gaining a better insight of the plankton diversity of these environments, in November 2012, the composition of the smallest size fraction of the eukaryotic plankton of the Rancho Hambre pools was analysed by means of Illumina HiSeq massive sequencing applied to the v9 region of the eukaryotic SSU rRNA gene (Lara et al. 2015). After obtaining and treating sequences, a total of 783 OTUs were finally kept for statistical analysis. Chrysophyceae-related sequences dominated all pools except RH2, in which the parasitoid clade Perkinsea had the highest proportion of sequences. Other clades standing for different nutrition modes (phagotrophic ciliates and bicosoecids, autotrophic chlorophytes and boldo-phyceae, osmotrophic fungi) were also well represented.

The five pools were classified using an unsupervised random forest analysis on the basis of environmental parameters, resulting in a dendrogram which clustered together minerotrophic RH1 and RH4 on one hand, and ombrotrophic RH3, RH5 and RH2 on the other. As this clustering matched the one obtained by GUniFrac analysis of community composition, indicator values of trophic conditions were calculated for each OTU using the IndVal method. Analysis of the 5% most characteristic OTUs for (i) minerotrophic and (ii) ombrotrophic pools showed that amongst pigmented organisms (phytoplankton), mixotrophic indicator OTUs were far more represented in ombrotrophic pools than in minerotrophic ones (15 and 3 OTUs, respectively), whilst strictly phototrophic organisms were more indicative of minerotrophic water bodies (5 and 1 OTUs). Also, many sequences of the highly diverse Chrysophyceae were good indicators of trophic conditions, whilst OTUs from minerotrophic pools represented colourless, heterotrophic clade F, and would account for many of the HFs formerly observed by Quiroga et al. (2013), Chrysophyceae from pigmented, mixotrophic clade E were indicators of ombrotrophic pools together with colourless bacterivorous Bicosoecida, in agreement with previous findings by Lara et al. (2011) for a Swiss peat bog. In all, these new results agreed well with the hypothesis of different metabolic pathways characterising large, minerotrophic pools and small, ombrotrophic ones proposed by Quiroga et al. (2013).

Remarks and future prospects

Peatlands are globally regarded as key actors of climatic change, since their ecosystem functioning which involves a high capacity to act as atmospheric carbon sinks, depends in turn on climatic conditions driving water table depth (Lindsay 2010). Also, the responsiveness of their biota to such climate-driven conditions renders them excellent sentinels of climate change. In particular, the peat bogs of Tierra del Fuego have allowed researchers to accurately reconstruct the climate dynamics of the late Holocene by inferring climate-driven changes in water table depth through the analysis of the testacean community (van Bellen et al. 2015). In this review, we took the Rancho Hambre peat bog as a study case in order to investigate the environmental features driving community structure and trophic web organisation within peat bog pools and their dependence on climatic variables. In agreement with the observations of Puglisi et al. (2014), hydrology of this ombrotrophic peat bog was primarily controlled by precipitation and evaporation processes. Landscape-driven features such as pool morphometry and hydrological connectivity showed strong interactions with meteorological variables such as temperature and precipitation, and characterised pools according to size and trophic status, as proposed in an interpretation model. Such environmental diversity explained much of the high biodiversity typically recorded in peatlands (Beadle, Brown, and Holden 2015).

The simultaneous analysis of different plankton communities allowed identifying common patterns of seasonal turnover and spatial distribution. The latter, together with differences in trophic web structure, strongly suggested that distinct metabolic pathways operate in minerotrophic and ombrotrophic pools, with a clear dominance of mixotrophic organisms in the latter. Significantly poorer plankton communities across different taxonomic groups and trophic compartments evidenced a stronger environmental filtering in ombrotrophic pools. This result, obtained by traditional plankton research techniques was highly consistent with those obtained by NGS diversity analysis of bacteria and small eukaryotes, and further supported by the evidence of bacterial phylogenetic clustering in these environments.

Another robust result of these investigations is that the plankton communities studied here are good indicators of environmental conditions, either through their community structure (CCA analyses), or by hosting taxa of high indicator value (IndVal analyses). It is therefore expected that they will be relevant indicators of climate-driven changes in temperature and hydric balance, since these rule concentration-dependent chemical features. Also top-down driven changes in the structure of trophic webs

can be expected, as temperature strongly affects growth and development of top-level crustaceans.

Recent climate changes in Tierra del Fuego lead to receding of glaciers around Ushuaia and lessening of accumulated snow during winter. This trend is expected to continue in the future, with a sensible reduction of water availability in summer (Iturraspe 2010) which would lead to dryer, more ombrotrophic conditions in the pools. Both increasing temperatures and lower water tables might lead to peat degradation (Kayranli et al. 2010) which would in turn feedback on climate change (Pena 2009). Nonetheless, these effects are not straightforward and can be mediated by biotic interactions: according to Breeuwer et al. (2010) higher temperatures and related enhanced nitrogen availability would have a positive effect on *Sphagnum* growth, yet competition with vascular plants would ultimately lead to peat-forming *Sphagnum* loss as predicted by models running for up to 100 years. It is in this complex scenario that highly sensitive, rapidly changing plankton communities would be most valuable as early alerts of climate-related environmental changes in peat bogs.

Acknowledgements

I am much indebted to all partakers in the Tierra del Fuego peat bog research projects dealt with in this review. The Dirección de Recursos Hídricos de la Provincia de Tierra del Fuego and the Centro Austral de Investigaciones Científicas (CAD-IC) contributed much valued logistic support. An anonymous referee provided insightful comments on a previous version of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author.

Funding

The research projects discussed in this article were funded by the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT) under Grant PICT 2006–1697; Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET) under Grant PIP 2010- 0050; and by MINCyT (Argentina) and DSA (South Africa) under Project SA-11–12.

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